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## Beaver-induced spatiotemporal patch dynamics affect landscape-level environmental heterogeneity

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## Abstract

Beavers (*Castor* sp.) are ecosystem engineers that cause significant changes to their physical environment and alter the availability of resources to other species. We studied flood dynamics created by American beaver (*C. canadensis* K.) in a southern boreal landscape in Finland in 1970–2018. We present for the first time, to our knowledge, a temporally continuous long-term study of beaver-induced flood disturbances starting from the appearance of beaver in the area. During the 49 years, the emergence of new sites flooded by beaver and repeated floods (61% of the sites) formed a dynamic mosaic characterized by clustered patterns of beaver sites. As beaver dispersal proceeded, connectivity of beaver sites increased significantly. The mean flood duration was approximately three years, which highlights the importance of datasets with high-temporal resolution in detecting beaver-induced disturbances. An individual site was often part of the active flood mosaic over several decades, although the duration and the number of repeated floods at different sites varied considerably. Variation of flood-inundated and post-flood phases at individual sites resulted in a cumulative number of unique patches that contribute to environmental heterogeneity in space and time. A disturbance mosaic consisting of patches differing by successional age and flood history is likely to support species richness and abundance of different taxa and facilitate whole species communities. Beavers are thus a suitable means to be used in restoration of riparian habitat due to their strong and dynamic influence on abiotic environment and its biotic consequences.

## 1. Introduction

In forest ecosystems, environmental heterogeneity is considered as an important factor promoting biological diversity. Environmental heterogeneity arises from variation in abiotic and biotic conditions, such as land cover, vegetation and topography (Kuuluvainen 1994, Esseen *et al* 1997, McCarthy 2001, Stein *et al* 2014, Stein and Kreft 2015). The role of organisms in creating heterogeneity has received increased attention during the past three decades. Ecosystem engineers are species that cause significant changes to their physical environment and directly or indirectly modulate the availability of resources to other species. They can alter the distribution and abundance of different species and thus, have important impacts on biodiversity (Jones *et al* 1994, 1997,

Bruno *et al* 2003, Wright *et al* 2004, Hastings *et al* 2007, Romero *et al* 2015, Rozhkova-Timina *et al* 2018).

Eurasian beaver (*Castor fiber* L.) and American beaver (*Castor canadensis* K.) are referred to as ecosystem engineers (Wright *et al* 2002, 2004, Johnston 2017). Beavers are large semi-aquatic rodents that inhabit freshwater streams and lakes, and alter the physical environment by cutting trees, building dams on the flowing water, and digging canals. Beaver ponds turn terrestrial riparian areas to aquatic systems creating a significant disturbance both at patch and landscape levels (1988, Johnston and Naiman 1990a, Collen and Gibson 2001, Wright *et al* 2004, Nummi and Kuuluvainen 2013, Hood and Larson 2015). Flooding kills the trees, widens the extent of riparian wetlands, and alters physical, chemical and

biological conditions of the site (Vehkaoja *et al* 2015, Ecke *et al* 2017, Johnston 2017, Nummi *et al* 2018). Beavers occupy a certain pond from a few years to several decades (Johnston and Naiman 1990a, Hyvönen and Nummi 2008). After the pond drains, a beaver meadow is formed as the exposed riparian sediments are colonized by grasses, herbs and shrubs (Johnston 2017). Later, a riparian forest is established unless beavers impound the stream again and a new flood resets the succession (Remillard *et al* 1987, Snodgrass 1997, Johnston 2017, Nummi *et al* 2018).

As a disturbance factor, beavers differ from fire and storm by being more predictable actors in the landscape (Wright *et al* 2002, Nummi and Kuuluvainen 2013). In boreal forests, beaver-induced disturbances occur in relatively stable low-lying wetland areas that rarely experience other types of larger natural disturbances. Beaver flooding leads to multi-tree mortality, or even to stand replacement, and can create large amounts and diverse forms of deadwood which is a key resource for numerous forest species (Esseen *et al* 1997, Nummi and Kuuluvainen 2013, Thompson *et al* 2016). Flood-inundated sites characterized by a littoral zone with a wide margin of shallow water and a broad belt of emergent plants and twigs create unique habitats in boreal landscapes (Nummi 1989, Nummi and Hahtola 2008). Beaver-induced floods have been reported to facilitate, for example, landscape-level plant species richness (Wright *et al* 2002, Bartel *et al* 2010), calicioid diversity (Vehkaoja *et al* 2017), butterfly populations (Bartel *et al* 2010), fish and amphibian communities (Snodgrass and Meffe 1998, Schlosser and Kallemeyn 2000, Dalbeck *et al* 2007), water bird breeding and diversity (Nummi and Hahtola 2008, Nummi and Holopainen 2014, Nummi *et al* 2019b), occurrence of woodpeckers (Pietrasz *et al* 2019), bat foraging (Nummi *et al* 2011), as well as species richness and abundance of terrestrial and semi-aquatic mammals (Nummi *et al* 2019a).

Our long-term understanding of the fluvial and wetland dynamics is somewhat biased, as it is based to a large degree on the environments lacking beaver (Butler 2006, Nummi and Kuuluvainen 2013). Eurasian beaver and American beaver were driven nearly to extinction between the 16th and 19th centuries mainly due to overhunting, and consequently, most of their impacts on riparian ecosystems were also lost. Protection, natural spread and reintroduction have led to a strong recovery of populations during the 20th century (Halley and Rosell 2002, Halley *et al* 2012, Parker *et al* 2012, Vehkaoja 2016, Law *et al* 2017).

Spatiotemporal knowledge of beaver-induced floods is a prerequisite in understanding the role of beaver as an agent creating and maintaining wetlands and influencing forest disturbance dynamics. Long-term dynamics of beaver-induced disturbances in the fluvial systems and riparian zone have been

typically studied by detecting beaver dams and ponds from aerial photography (Naiman *et al* 1986, 1988, Broschart *et al* 1989, Johnston and Naiman 1990a, 1990b, Meentemeyer and Butler 1995, Snodgrass 1997, Wright *et al* 2002, Martell *et al* 2006, Hood and Bayley 2008, Green and Westbrook 2009, Little *et al* 2012, Martin *et al* 2015, Levine and Meyer 2019). However, as only a restricted number of photographs has been available over the study periods examined, no long-term spatial analyses of beaver sites have been carried out with temporally consistent datasets. Demmer and Bechsta (2008) field-inventoried beaver dams for 17 years, but individual sites were not studied in the detailed spatiotemporal context. Impacts of beaver on the landscape structure and habitat availability have been studied mainly in North America (e.g. Johnston and Naiman 1990a), whereas such knowledge is scarce in Europe (but see e.g. Hyvönen and Nummi 2008, Willby *et al* 2018), where research has more focused on population trends and habitat selection by beaver (e.g. Hartman 1995, 1996, Fustec *et al* 2001, John *et al* 2010, Zwolicki *et al* 2019).

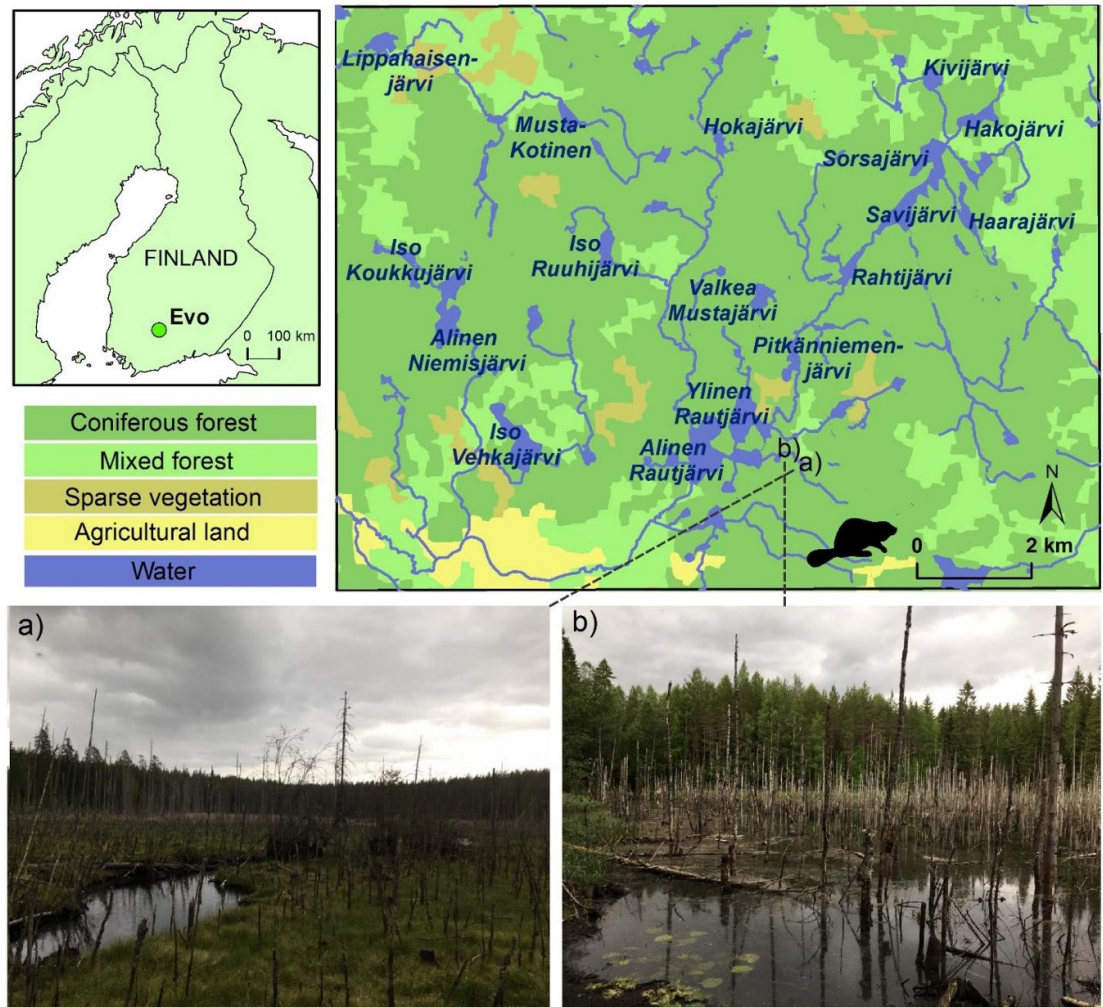
We studied beaver-induced patch dynamics using a unique long-term observation data (1970–2018) on beaver sites in a southern boreal forest landscape in Finland. American beaver was introduced in the region in the 1950s, after the absence of beavers in Finland since 1868 (Parker *et al* 2012). We present for the first time, to our knowledge, a detailed study of beaver-induced disturbance dynamics starting from the appearance of beaver in the boreal forest landscape. Specifically, we focus on the following questions: (1) How do the abundance and spatial patterns of beaver sites (flooded and post-flood) evolve over time? (2) How do the beaver sites vary spatially and temporally in terms of successional age and flood history? (3) How do the beaver sites contribute to the environmental heterogeneity of the forest landscape?

## 2. Material and methods

### 2.1. Study area

The study area ( $A = 136 \text{ km}^2$ ) is located in the Evo region, Finland (figure 1). The area belongs to the southern boreal vegetation zone (Ahti *et al* 1968) and is predominantly coniferous with deciduous patches scattered in the landscape. Wooded and open mires occur sporadically in the region. Most of the area is used for forestry purposes. There has been some small-scale prescribed burning, but this has been on the drier sites and has not affected the riparian forests (Nummi and Kuuluvainen 2013, Thompson *et al* 2016). Protected areas cover approximately 7% of the total area. Agricultural land occurs to a limited extent mainly in the southern part of the region. No major land use changes have taken place during the past decades in the studied sites.

The mean annual air temperature in the region is  $4.2^\circ\text{C}$  and the total annual precipitation sum is



**Figure 1.** The location of the study area, the main land cover classes (Corine Land Cover 2018; Source: National datasets (20 m) SYKE (partly LUKE, MAVI, LIVI, VRK, EU, NLSF Topographic database 01/2017), and lakes and watercourses (Source: National Land Survey of Finland, Topographic database 10/2019). Examples of (a) a post-flood site four years since a prior (2nd) flooding and (b) a site flooded since 2006. Photos: Sonja Kivinen (June 2018). See also figure 2 for aerial photography.

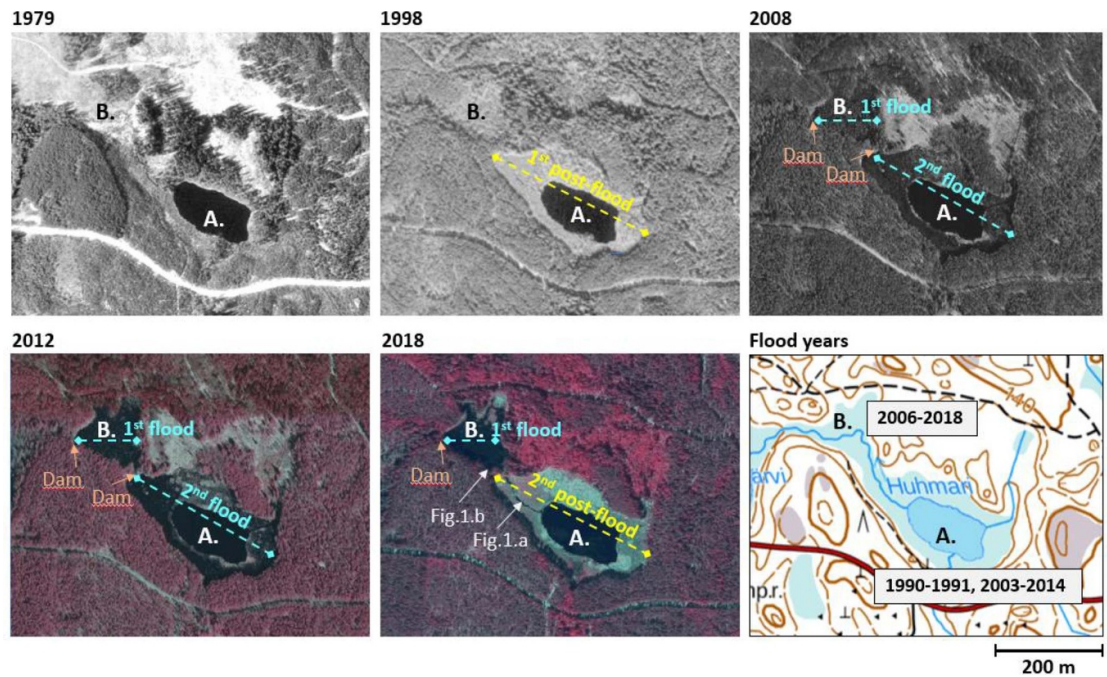
645 mm (Hämeenlinna Lammi Pappila observation station; Pirinen *et al* 2012). No significant long-term trends in annual or seasonal mean precipitation has been observed in the area (Jylhä *et al* 2014, Ruoho-Airola *et al* 2014). Most of the region consists of sandy glacial deposits, and the elevation varies between 97 m and 197 m. There are 184 lakes and ponds in the study area (figure 1). A majority of them are brown-colored forest lakes (Arvola *et al* 2010) with the mean size of 3.6 ha. A total length of the rivers and streams is approximately 102 km and their width commonly vary between 2–5 m.

American beaver (*Castor canadensis* K.) was introduced in the region in 1957. The number of beaver colonies during recent years ranged from three to nine. Data on the locations, emergence and duration of floods in the study area were based on the long-term observation data collected by visiting at beaver sites. The ponds and the presence of a dam were checked by walking. During 1970–1987 beaver activity in the area was recorded within other field

activities of the Evo Game Research Station, from 1988 onwards most of the lakes were visited in a long-term duck project (Nummi *et al* 2019b) (see Acknowledgments).

Beavers typically dammed the outlet of a small lake or pond, resulting in the flood in the riparian zone (Hyvönen and Nummi 2008). The amount flooding varied considerably in the study area. Sometimes only a flooded sector of 1–2 meters were formed on the shore, sometimes an area of a size of the original pond was flooded, comprising 1–2 hectares. Typically, the water level rose 50–100 cm. The flooded area extended up to 50 m from the shoreline (Nummi and Hahtola 2008). In a stream pond there typically were more large trees standing in the flooded water, because the trees grew more near to the original water edge. The area of water also increased proportionally more in stream beaver ponds. American and Eurasian beaver (*Castor fiber* L.) have been shown to have a similar effect on wetland ecosystems (Danilov and Fyodorov 2015).





**Figure 2.** Flood dynamics at two beaver sites illustrated by aerial imagery acquired between 1979 and 2018 (1979–2008: black-and-white imagery, 2012–2018: false-color imagery) (Source: National Land Survey of Finland, Orthophotos 10/2019). The year 1979 image shows the initial situation before beaver floods. Dark areas in the images are water. Post-flood areas in the site A are light gray (1998) and light cyan color (2018). The area of the lake prior flooding (A) is 1.0 ha. A topographic map from the National Land Survey of Finland Topographic map series 10/2019. See figures 1(a) and (b) for photos of the sites.

## 2.2. Spatial analyses

Spatial analyses were carried out using ArcMap 10.5 (Esri). The total number of beaver sites (flooded and post-flood) within the study area and the number of repeated floods at each site were calculated for years 1970–2018. A repeated flood occurs when the same site is dammed again. The geomorphology of the area is such, that riparian areas surrounding the ponds narrows down in a way where there is a clear ‘economic’ spot for dam building. This is exemplified in the dam of the pond A. in figure 2. The earlier dam between 1979 and 1998 was at exactly the same place. In a few, mostly riverine, instances, there has been a slight variation in dam places, but this does not affect the general picture. The duration of flood phases and post-flood phases were calculated for each site. A flood phase consisted of one or more consecutive years when the site was flood-inundated. Similarly, a post-flood phase was defined as the time period when the dam had breached and the site was drained. In order to study the successional age of post-flood patches, years since prior flood (YSPF) was calculated for each site.

Two beaver sites can have very different flood history, which in turn, can affect the environmental characteristics of the site. In order to describe spatiotemporal dynamics of the flood mosaic, flood history for each individual beaver site was determined. Sites were classified into different flood history types based on the current flood status (flooded or post-flood) and the successional order of the flood. A total

of 15 different flood history types (no flood, 1st–7th flood and 1st–7th post-flood) occurred in the study area during the 49 years. Figure 2 shows an example of flood dynamics at two beaver sites in 1979–2018.

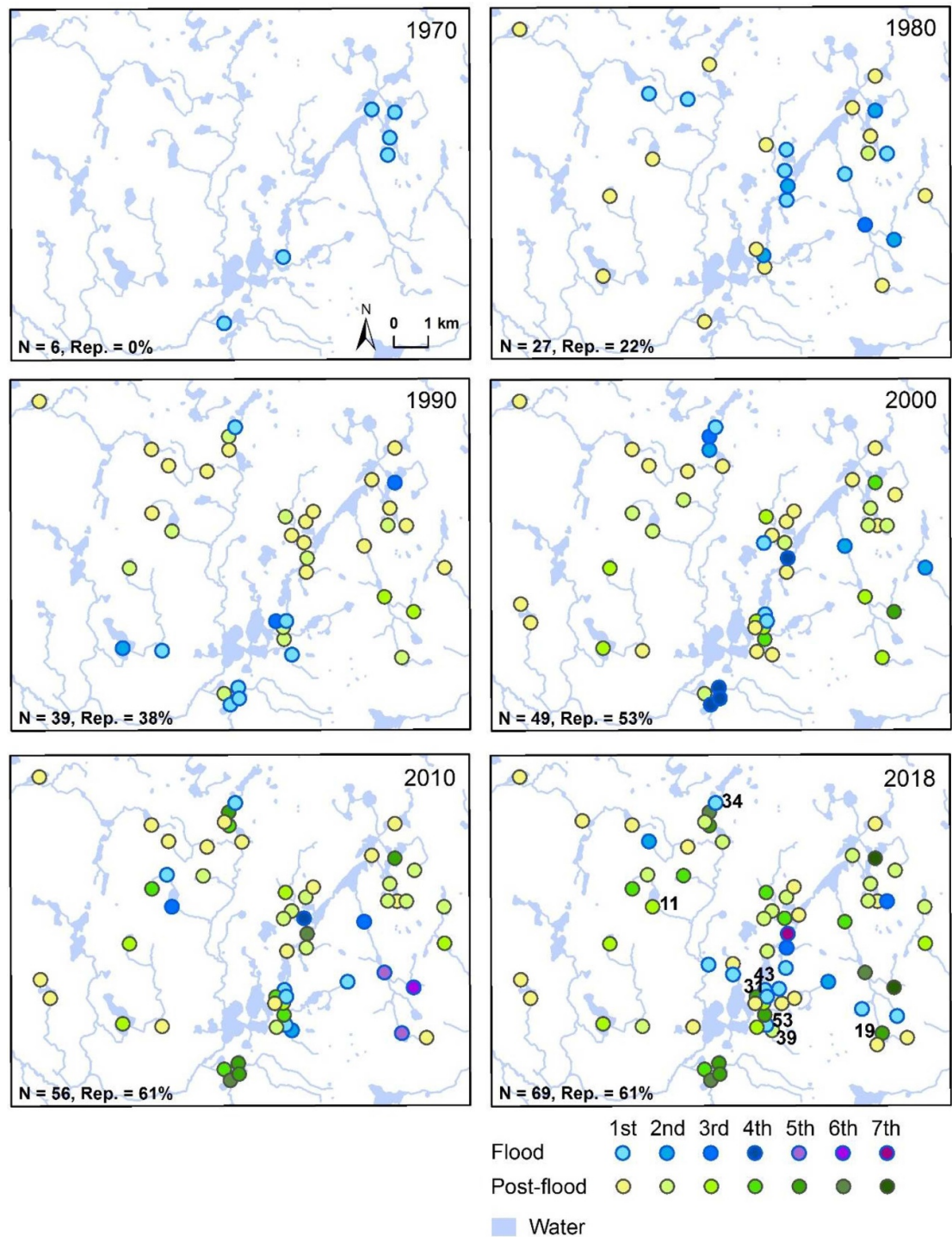
Flood history diversity was studied using a Shannon Diversity Index calculated in the following way (Shannon 1948):

$$H = - \sum_{i=1}^s p_i * \ln p_i$$

where  $s$  is the total number of flood history types in the landscape,  $p_i$  is the proportion of all beaver sites represented by flood history type  $i$ .

The index was calculated separately for each study year including in the analysis a total of 69 beaver sites that had emerged by 2018.

Spatial distribution of beaver sites was examined by measuring the distance between the center point of each site and its nearest neighboring site. Using these data, the mean distance to the nearest neighboring beaver site and the standard deviation of distances was then calculated. The Nearest Neighbor Index (NNI) was calculated to measure the spatial distribution of a beaver site pattern within the study area. NNI is expressed as the ratio of the observed distance divided by the expected distance (the average distance between neighbors in a hypothetical random distribution). If the index is less than 1, the pattern exhibits



**Figure 3.** Occurrence of beaver sites (flooded and post-flood), classified by number of floods since 1970. Maps shown at approximately decadal intervals, 1970–2018. Lakes and watercourses from the National Land Survey of Finland Topographic database 10/2019. N = the total number of beaver sites, Rep. = the proportion of repeatedly flooded sites of all beaver sites. The locations marked with numbers in the 2018 map are beaver sites where the duration of an individual flood phase was  $\geq 10$  years. The site number 39 is A and the site number 53 is B in figures 1 and 2. See also figure 4. for detailed flood phase information.

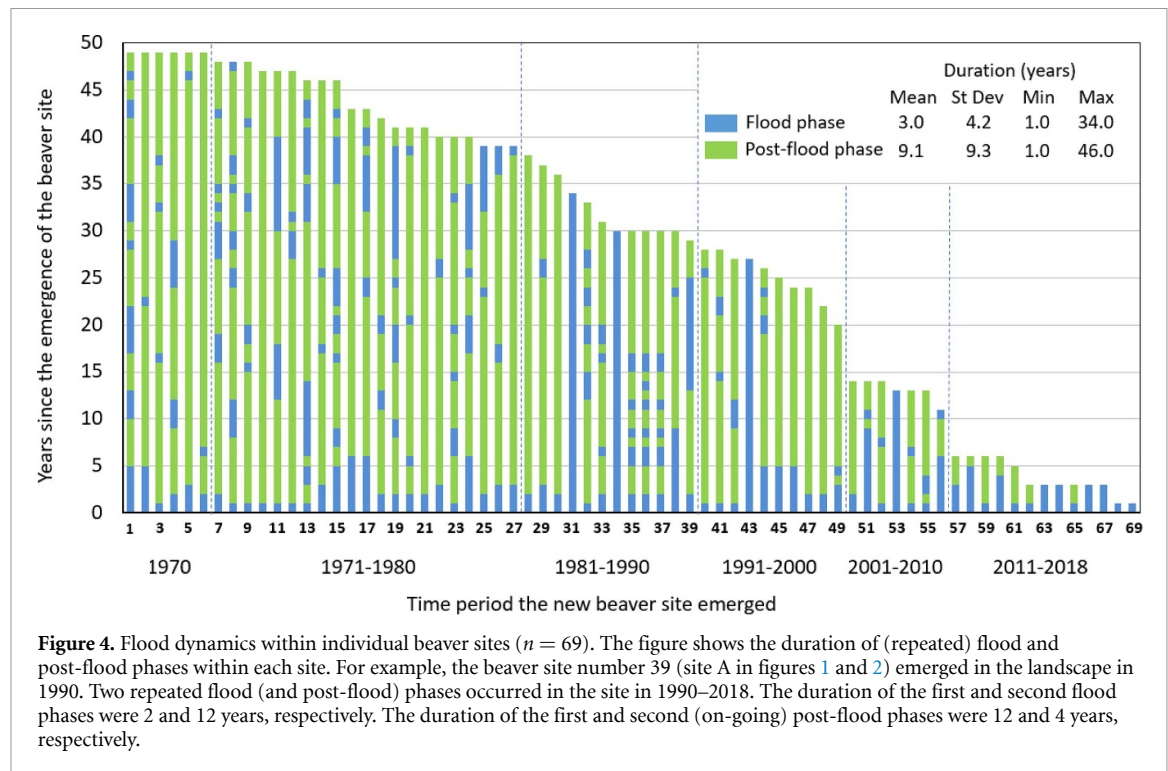
clustering. If the index is greater than 1, the trend is toward dispersion.

Landscape connectivity is determined by interactions between the spatial structure of the landscape and the movement behavior of species (Tischendorf and Fahrig 2000). Connectivity for beaver sites was measured using a connectivity index  $S_i$  (Hanski 1994, Moilanen and Hanski 2001), which is given by the

sum of contributions of all beaver sites:

$$S_i = \sum \exp(-\alpha d_{ij}) A_j$$

where  $d_{ij}$  is the distance between beaver sites  $i$  and  $j$ ,  $A_j$  is the area of beaver sites.  $A$  was given a value 1 ha for all sites as the size of the flooded area was not known.



**Figure 4.** Flood dynamics within individual beaver sites ( $n = 69$ ). The figure shows the duration of (repeated) flood and post-flood phases within each site. For example, the beaver site number 39 (site A in figures 1 and 2) emerged in the landscape in 1990. Two repeated flood (and post-flood) phases occurred in the site in 1990–2018. The duration of the first and second flood phases were 2 and 12 years, respectively. The duration of the first and second (on-going) post-flood phases were 12 and 4 years, respectively.

Because no specific species was studied, the parameter  $\alpha$  was given a value 1.

In order to study local characteristics of the beaver site mosaic, site abundance (SA) expressing the number of beaver sites on a buffer zone basis was calculated. Buffer zones with the radius of 500, 1000, 1500, and 2000 m were calculated around each beaver site and the total number of sites was measured within the buffer area ( $n = 1$ ; a central beaver site only,  $n = 2$ ; a central beaver the site and one neighbor etc.).

### 3. Results

#### 3.1. Spatiotemporal distribution and flood history of sites

The number of beaver sites (flooded and post-flood) increased from six sites in 1970 to 69 sites in 2018 (figure 3). Beavers flooded annually 0–6 new, previously non-flooded sites (figure 4). The abundance of flood sites increased steadily with on average 13 new sites per decade. In 2018, 51 of the beaver sites were lakes and 18 were riverine/wetland environments. A total of 28% of the lakes in the study area were flooded by 2018.

About 61% of the studied sites were repeatedly flooded by 2018 (figures 3 and 4). Of these repeatedly flooded sites ( $n = 42$ ), 38% were flooded twice, 33% were flooded 3–4 times and 29% were flooded 5–7 times. The mean duration of a flood phase was 3 years, and 90% of floods lasted 1–5 years. An exceptionally long flood phase lasting  $\geq 10$  years occurred in seven sites. The mean duration of a post-flood phase was 9 years. Nearly half of the post-flood phases lasted 1–5 years, and 36% and 16% of the post-flood

phases lasted 6–15 years and 16–46 years, respectively (figure 4).

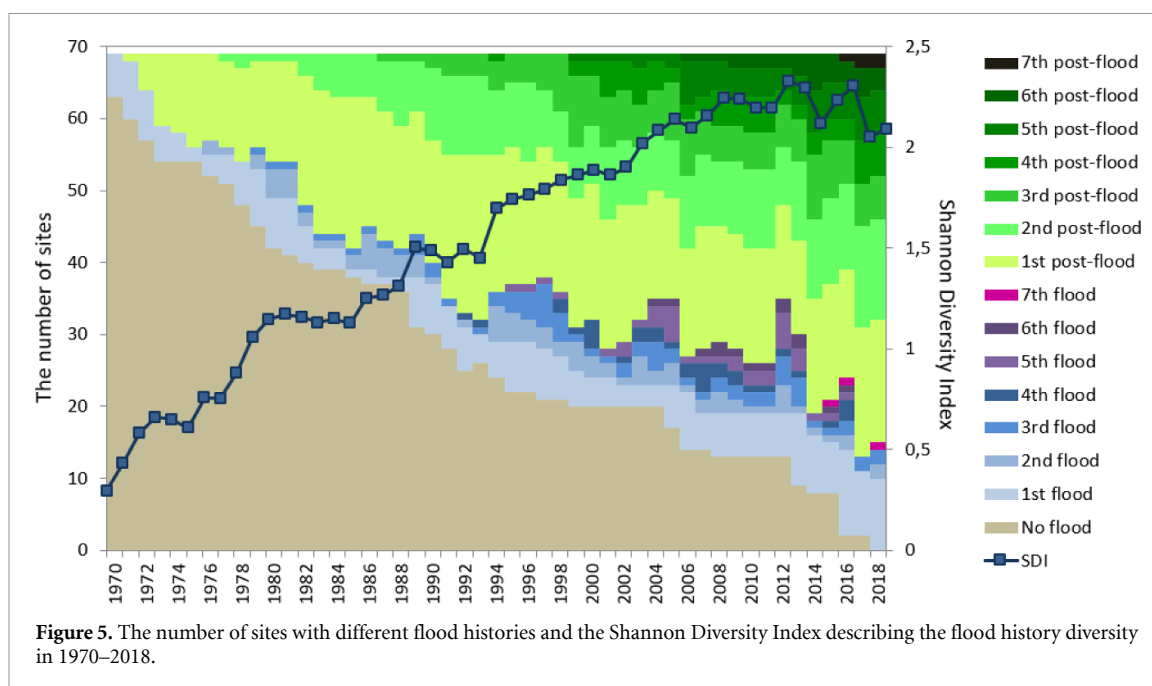
The Shannon Diversity Index calculated to investigate the diversity of different flood history types (not flooded, 1st–7th active flood phases, 1st–7th post-flood phases) at landscape level increased relatively steadily from 0.30 in 1970 to 2.33 in 2012. By 2018, the diversity of flood history types slightly declined to 2.09 (figure 5).

The mean distance to the nearest neighboring beaver site declined from 1.25 km in 1970 to 0.59 km in 2018 (table 1). Beaver sites had sparse, but widespread occurrence during the early dispersal of beaver in the landscape (1980: NNI = 0.95). New floods often occurred in the vicinity of the earlier flooded sites. ‘Hot spots’ of spatially clustered beaver sites occurred particularly along the lake-river network in the central part of the study area (figure 3), which is also observed in NNI values indicating clustered patterns (table 1). The mean connectivity of beaver sites increased from 0.87 in 1970 to 4.81 in 2018. The connectivity values of individual patches measured within the same time period varied notably reflecting the fact that the beaver site network consisted of both highly clustered as well as isolated patches. The mean site abundance measured within 0.5–2 km buffer zones increased from 1.3–3.0 sites in 1970 to 2.2–10.9 sites in 2018 (table 1).

#### 3.2. Variation in successional age of beaver sites

Figure 6 shows the annual number of flooded sites and post-flood sites. Post-flood sites were grouped according to the years since the prior flooding





**Figure 5.** The number of sites with different flood histories and the Shannon Diversity Index describing the flood history diversity in 1970–2018.

**Table 1.** Spatial distribution, connectivity and local abundance of beaver sites. NN = the distance to the nearest neighboring beaver site (km), NNI = Nearest Neighbor Index,  $S_i$  = Connectivity Index, SA = Site abundance within different buffer zones.

Year	NN (km)		NNI	$S_i$	St. Dev.	SA			
	Mean	St. Dev.		Mean		0.5-km Mean	1-km Mean	1.5-km Mean	2-km Mean
1970	1.25	0.94	0.52	0.87	0.61	1.33	2.33	3.00	3.00
1980	1.06	0.83	0.95	1.69	0.96	1.37	2.26	3.22	4.56
1990	0.71	0.59	0.76	2.46	1.09	1.82	3.21	4.13	5.72
2000	0.65	0.55	0.78	3.26	1.59	2.18	4.02	5.41	7.12
2010	0.61	0.51	0.79	3.72	1.76	2.21	4.32	6.00	8.25
2018	0.59	0.38	0.84	4.81	2.51	2.22	4.91	7.75	10.91

(successional age). The annual number of flood-inundated sites varied from 2 to 22, and their proportion of all beaver sites was on average 30%. The diversity of post-flood sites of different successional ages increased noticeably during the study period. Figure 7 illustrates the increase of the number and diversity of beaver sites of different successional age in the landscape in 1970–2018. This diversity arises both from the emergence of new flooded sites and flood dynamics at individual sites including the repetition of active flood phases and post-flood phases of various durations.

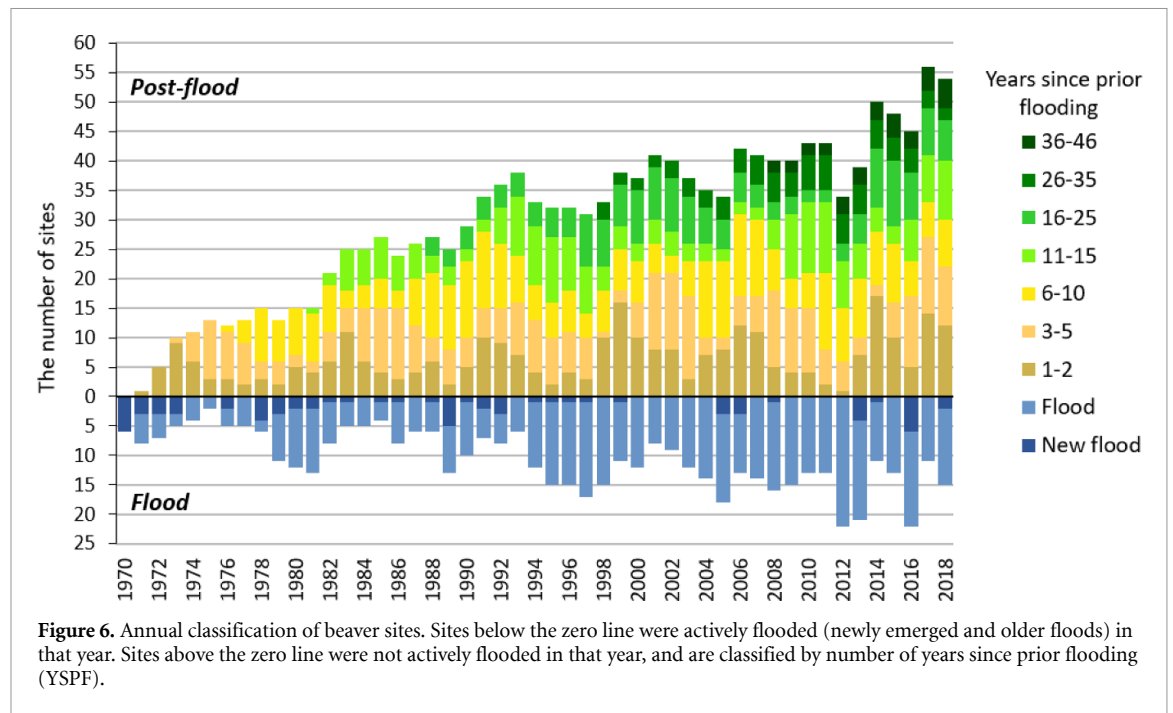
#### 4. Discussion

Our temporally consistent data on beaver-induced floods over nearly a half century enabled a detailed spatial analysis of flood dynamics both at landscape and patch level. The emergence of new floods and repeated floods formed a constantly evolving and expanding flood site mosaic. Variation of flood-inundated and post-flood phases at individual sites resulted in a cumulative number of unique patches

that contribute to spatial and temporal heterogeneity of the forest landscape.

Beaver-induced floods exhibited clustered spatial patterns in the study area. This finding is in line with earlier studies showing that distant sites are often colonized before nearer sites and that beaver colonies began to cluster as new sites are occupied by dispersers from earlier colonized sites (Fustec *et al* 2001, John *et al* 2010, Martin *et al* 2015). This spatial organization of flood sites reflects the fact that beavers are highly territorial animals and that they establish colonies first in optimal habitats (Naiman *et al* 1988, Fustec *et al* 2001, John *et al* 2010, Bloomquist *et al* 2012, Martin *et al* 2015). The habitat suitability for beavers is determined by several physical variables, such as watercourse width and gradient, together with resource availability (Fustec *et al* 2001, John *et al* 2010, Stringer *et al* 2018). Earlier floods may also create more suitable wetland habitat in the neighborhood that can further promote the clustering of beaver sites (Martin *et al* 2015). For example, the results of Hyvönen and Nummi (2008) indicated that even a short-term beaver-induced flood (1–2 years) can





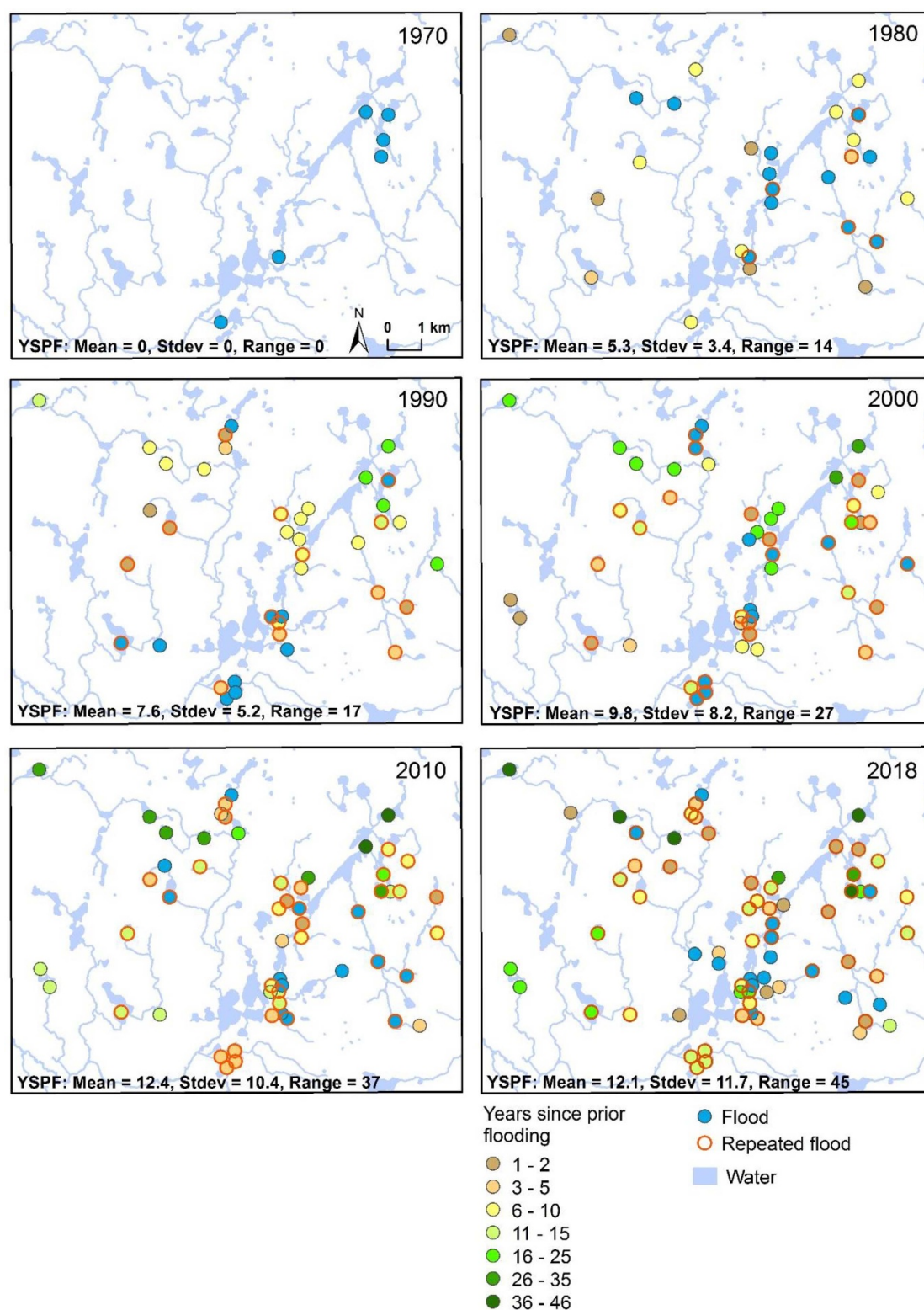
change tree species composition towards the dominance of deciduous trees favored by beavers.

Flood dynamics varied considerably among the sites from locations with only a single flood to locations with up to seven repeated floods during the study period. In other words, beaver sites in the landscape have different flood histories. Productive sites with plentiful deciduous trees are preferred by beavers, and are likely to become repeatedly flooded, whereas less suitable sites may be abandoned more quickly or never ponded (Naiman *et al* 1988, Fustec *et al* 2001, Fryxell 2001, Hyvönen and Nummi 2008, Martin *et al* 2015, Vehkaoja *et al* 2015). In this shifting mosaic of patches, new flood inundated sites emerge, while plant succession proceeds in earlier flooded, abandoned sites. In addition to this, a notable number of sites were repeatedly flooded, which implies that once a new flood occurs in the landscape, the site may be a part of the active flood mosaic over several decades. In our study area, nearly half of the post-flood phases lasted 1–5 years. During such relatively short post-flood phases, a beaver meadow characterized by herbs and grasses is formed. The mean duration of a post-flood phase was 9 years. Hyvönen and Nummi (2008) found that in beaver sites abandoned 5–15 years ago, coniferous trees were particularly susceptible to flooding, and deciduous trees dominated during succession. Regeneration (density and maximum length of the trees) showed no clear pattern in relation to the duration of the post-flood phase. It should be noted that plant succession within post-flood sites has been reported to be slower than after other disturbances, such as fire (Terwilliger and Pastor 1999). This further strengthens the long-term impacts of

beaver-disturbances on landscape structure and composition.

The mean connectivity of beaver sites increased 5.5-fold during the study period. Similarly, the local site abundance increased by 1.7–3.6-fold within 500–2000 m buffer zones. From the metapopulation perspective (Hanski and Ovaskainen 2000), connectivity of habitat networks created by beavers have important implication on the populations of numerous species associated with aquatic environments, wetlands and deadwood. For example, Cunningham *et al* (2007) found that sites with high amphibian species richness were best predicted by connectivity of wetlands through stream corridors and wetland modification by beaver, as beaver enhance connectivity by reducing the distances among suitable breeding and potential foraging sites (see also Hood and Larson 2015). Furthermore, the recurring floods maintain the continuity of deadwood networks in the landscape. This may facilitate a wide scope of deadwood dependent species in areas where deadwood is scarce due to intensive forest management (Esseen *et al* 1997). Furthermore, in reflooded patches there might present different sized deadwood resulting from consecutive floods. This further increases the value of the patch for organisms living on deadwood (Thompson *et al* 2016).

The flood mosaic was characterized by relatively young flood and post-flood sites in the beginning of the study period. In 2018, successional age of flood sites and post-flood sites varied between 1 and 34 years and 1 and 46 years, respectively. Increasing successional age range over time indicates the increasing diversity of patches with varying abiotic and biotic conditions. This can have important implications for habitat availability for different taxa and thus, species



**Figure 7.** Occurrence of beaver sites, classified as in figure 6. Maps shown at approximately decadal intervals, 1970–2018. Lakes and watercourses from the National Land Survey of Finland Topographic database 10/2019. The figure also shows the mean, standard deviation and range of YSPF calculated for post-flood sites in the landscape.

richness and composition in the landscape (Stringer and Gaywood 2016).

Nummi and Holopainen (2014) found the most substantial increase in the number of water birds during the first two years of flooding, although the beneficial effect of beaver-induced flood on diversity

lasted the whole period of inundation. Fish species richness was reported to be highest in ponds 9–17 years old in headwater streams (Snodgrass and Meffe 1998). Russell *et al* (1999) found that amphibian community diversity was similar among new ( $\leq 5$  years) and old ( $\geq 10$  years) beaver ponds, whereas

the richness and total abundance of reptiles were significantly higher at old beaver ponds than at new beaver ponds. Bonner *et al* (2009) reported that the oldest beaver ponds (>56 years) had twice as many rare plant species as the youngest ponds ( $\leq 6$  years), whereas the youngest ponds had higher overall mean species richness than other ponds. Aznar and Desrochers (2008) found that abandoned beaver ponds had higher density of deciduous shrubs and graminoid cover and supported higher bird diversity than nearby riparian areas. The study of Bush *et al* (2019) showed that each successional stage of beaver wetlands has a different taxonomic make-up of invertebrate communities. Due to their strong and dynamic influence on abiotic environment and coupled biotic–abiotic processes, beavers are increasingly utilized for habitat restoration (Byers *et al* 2006, Willby *et al* 2018, Nummi and Holopainen 2020). Knowledge of the flood status and flood history within individual sites is crucial to estimate the potential ecological implications of the dynamic flood mosaic.

In our study area, about 90% of the active flood phases lasted 1–5 years. This highlights the importance of temporally continuous datasets in detecting and monitoring beaver-induced floods in the landscape. Aerial photography utilized in earlier studies are useful in mapping the spatial extent of floods and can provide a general estimate of beaver-induced disturbances in the region (Naiman *et al* 1986, 1988, Broschart *et al* 1989, Johnston and Naiman 1990a, 1990b, Meentemeyer and Butler 1995, Snodgrass 1997, Wright *et al* 2002, Martell *et al* 2006, Hood and Bayley 2008, Green and Westbrook 2009, Little *et al* 2012, Martin *et al* 2015, Levine and Meyer 2019). However, due to the limited availability of aerial photographs, only part of the changes in rapidly evolving flood mosaics could have been detected. New remote sensing techniques, such as unmanned aerial systems (drones) with high spatial resolution data can provide more efficient tools for monitoring beaver-induced floods and changes in the vegetation structure (Colomina and Molina 2014, Puttock *et al* 2015).

## 5. Conclusions

Beavers are returning to their former distribution range in Europe, where they were nearly extirpated centuries ago. This calls for deeper understanding of the impacts of beaver on various ecosystems, as they have been neglected as disturbance agents due to their long absence in the European landscapes. Our results showed that long-term beaver activity has created a dynamic mosaic of flood-inundated and post-flood patches differing by successional age and flood history. As beaver dispersal proceeded, clustering and connectivity of beaver sites increased. These networks consisting of dynamic patches with diverse abiotic and biotic conditions increase environmental heterogeneity in space and time. Our results highlight that

beaver-induced changes can influence ecosystems for decades, or even longer (Johnston 2015), especially if sites are repeatedly flooded. Better knowledge of the linkages between dynamics of beaver-created habitat patches and succession of populations of different taxa could significantly improve our understanding of the influence of beaver on terrestrial and aquatic biodiversity. Even now it is evident that beavers can be used as a suitable means for restoration of riparian habitat. The results of this study are applicable to other parts of Eurasia, where beaver re-establishment via dispersal and reintroductions is still ongoing.

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## Data availability statement

Any data that support the findings of this study are included within the article.

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